sensory cell stumps can survive without an ensheathing glial cell.

Our results are consistent with the recent finding that synaptic connections are selectively formed between isolated leech neurons placed next to one another in culture medium in the absence of glia (*15*). Such conditions are, however, quite different from those for axons regenerating in the intact animal.

What guides regenerating axons to their correct synaptic targets remains unknown. Previous experiments showed that the synaptic target is not necessary for correct growth of the S cell axon (*16*). Moreover, as in the CNS of other invertebrates and vertebrates, neurons and glia in the leech CNS have no basal lamina, an extracellular structure thought to direct the growth of regenerating motor axons in vertebrates (*17*). One possible guide for axon growth in the leech is the distal axon stump. The regenerating S axon can grow along its severed stump and can form electrical synapses with it (*7, 9*). The increased sprouting of some regenerating axons after the loss of glia suggests that glia guide or restrict axon growth. However, as our experiments show, the ensheathing glial cell is not required for accurate regeneration of axons and synapses in the leech CNS.

ELLEN J. ELLIOTT
KENNETH J. MULLER

Department of Embryology, Carnegie Institution of Washington, Baltimore, Maryland 21210

References and Notes

1. P. J. Reier and H. deF. Webster, *J. Neurocytol.* **3**, 591 (1974); J. E. Turner and M. Singer, *J. Exp. Zool.* **190**, 249 (1974); M. Murray, *J. Comp. Neurol.* **168**, 175 (1976).
2. S. Ramon y Cajal, *Degeneration and Regeneration in the Nervous System* (Hafner, New York, 1928); S. Ohmi, *Z. Zellforsch. Mikrosk. Anat.* **56**, 625 (1962).
3. C. Clemente, *Int. Rev. Neurobiol.* **6**, 257 (1964); A. J. Aguayo, R. Dickson, J. Trecarten, M. Attiwell, G. M. Bray, P. Richardson, *Neurosci. Lett.* **9**, 97 (1978); P. M. Richardson, U. M. McGuinness, A. J. Aguayo, *Nature (London)* **284**, 264 (1980); L. J. Stensaas, P. R. Burgess, K. W. Horch, *Neurosci. Abstr.* **5**, 684 (1979).
4. K. J. Muller, *Biol. Rev.* **54**, 99 (1979).
5. E. J. Elliott and K. J. Muller, *Brain Res.* **216**, 99 (1981).
6. I. Parnas and D. Bowling, *Nature (London)* **370**, 626 (1977); D. Bowling, J. Nicholls, I. Parnas, *J. Physiol. (London)* **282**, 169 (1978); S. A. Scott and K. J. Muller, *Dev. Biol.* **80**, 345 (1980).
7. K. J. Muller and S. Carbonetto, *J. Comp. Neurol.* **185**, 485 (1979).
8. R. E. Coggeshall and D. W. Fawcett, *J. Neurophysiol.* **27**, 229 (1964).
9. S. Carbonetto and K. J. Muller, *Nature (London)* **267**, 450 (1977).
10. J. K. S. Jansen and J. G. Nicholls, *Proc. Natl. Acad. Sci. U.S.A.* **67**, 636 (1972); B. G. Wallace, M. N. Adal, J. G. Nicholls, *Proc. R. Soc. London Ser. B* **199**, 567 (1977).
11. K. J. Muller and U. J. McMahan, *Proc. R. Soc. London Ser. B* **194**, 481 (1976).
12. M. R. Meyer and G. D. Bittner, *Brain Res.* **143**, 195 (1978); *ibid.*, p. 213.
13. D. C. Van Essen and J. K. S. Jansen, *J. Comp. Neurol.* **171**, 433 (1977).
14. E. J. Elliott, unpublished results.
15. D. F. Ready and J. G. Nicholls, *Nature (London)* **281**, 67 (1979); P. A. Fuchs, J. G. Nicholls, D. F. Ready, *J. Physiol. (London)* **316**, 203 (1981).
16. K. J. Muller and S. A. Scott, *Science* **206**, 87 (1979).
17. L. M. Marshall, J. R. Sanes, U. J. McMahan, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 3073 (1977); J. R. Sanes, L. M. Marshall, U. J. McMahan, *J. Cell Biol.* **78**, 176 (1978).
18. We thank B. Thomas for excellent technical assistance and A. Mason and R. Rohwer for helpful discussions and critical reading of the manuscript. Supported in part by a National Multiple Sclerosis Society postdoctoral fellowship to E.J.E. and by NIH grant NS 15014 to K.J.M.

25 September 1981; revised 27 November 1981

Territoriality and the Origin of Slave Raiding in Leptothoracine Ants

Abstract. *The slave-raiding behavior of* Harpagoxenus canadensis *closely resembles the territorial behavior of its host species,* Leptothorax muscorum. *Of primary importance is the discovery that both species of ants recruit nest mates into battle using an alarm-recruitment system which is a probable evolutionary precursor of more specialized forms of slave-raiding recruitment. The behavior of these species supports the hypothesis that slave raiding in leptothoracine ants evolved from territorial behavior.*

Slave-making ants are social parasites which supplement the labor force in their colonies by raiding other ant nests. Typically, the slave makers capture brood which is reared in their colonies to produce slave workers. Slavery is best known and most dramatic in its obligatory form, but less specialized forms of facultative intra- and interspecific slavery also occur (*1–3*). The evolutionary origin of ant slavery has been debated since the time of Darwin. However, slavery has evolved independently in several ant genera belonging to at least two subfamilies (*3*). Hence, a variety of evolutionary explanations may be necessary.

Among leptothoracine ants, two hypotheses have been advanced to explain the evolution of slave raiding. The territorial hypothesis maintains that slave raiding evolved from territorial fighting and opportunistic brood predation among colonies of closely related species (*2*). The alternative transport hypothesis contends that slave raiding evolved from brood transport among nests within colonies of a nonparasitic polydomous (multiple nests) and polygynous (multiple queens) species (*4*). Observations of the slave-raiding behavior of *Harpagoxenus canadensis* and of the territorial behavior of its host species, *Leptothorax muscorum*, as described in this report, support the territorial hypothesis.

The four species of the ant genus *Harpagoxenus* are morphologically well adapted for fighting. They are larger than their *Leptothorax* host species, with disproportionately larger heads and mandibles. In addition, inscribed on the dorsal surface of their heads is a pair of longitudinal grooves (scrobes) into which the antennal scapes can be folded for protection during fights. Both *H. americanus* and *H. sublaevis* have been shown to be obligatory slave makers (*5*), but *H. zaisanicus* and *H. canadensis* have been considered slave makers only by analogy and because they occur in mixed colonies with *Leptothorax* workers (*6, 7*). We collected colonies of *H. canadensis* and *L. muscorum* in northwestern Quebec. Interactions between *H. canadensis* and *L. muscorum* colonies ($N = 10$) and between pairs of *L. muscorum* colonies ($N = 6$) were observed in laboratory arenas (*8*).

During *H. canadensis* slave raids, members of opposing colonies were mutually antagonistic, with both slave makers and slaves being involved in the fighting. Even when outnumbered 2 to 1, slave-maker colonies consistently overwhelmed target colonies, raided their nests, and appropriated their broods. Workers and reproductives eclosed from captured brood. The workers remained as functional colony members (slaves), but the reproductives soon left in apparent attempts to conduct mating flights.

Interactions between *L. muscorum* colonies also always involved fighting. In four of six replicate experiments, the larger colony overran the smaller colony's nest and transported the captured brood back to its own nest, where it was mutilated and eaten. Colonies in the other two experiments coexisted for the duration of the experiment (3 days), apparently because the smaller colony erected a barricade of debris in its nest entrance. These observations indicate that *L. muscorum* colonies are territorial and capable of conducting territorial raids and engaging in opportunistic brood predation. The territorial hypothesis postulates that these behaviors were characteristic of the ancestors of lepto-

0036-8075/82/0305-1262$01.00/0

thoracine slave makers, and their discovery in a member of the subgenus from which *Harpagoxenus* is thought to have evolved (*4*) supports the territorial hypothesis.

Slave raids by *H. canadensis* and territorial raids by *L. muscorum* contain the four elements considered to be typical of slave-raiding behavior: scouting, recruitment, fighting, and brood transport (*3*). Moreover, in both species these elements occur in identical contexts and sequences. Slaves join in all aspects of the raids of slave makers; yet their behavior is virtually identical to that of free-living conspecifics during territorial raids. Significantly, the only difference observed was that slaves do not destroy captured brood.

Workers of both species scout individually and attack alien workers by biting. However, their fighting tactics are quite different. The *L. muscorum* workers fight by clamping their mandibles onto opponents and pulling. Fights may last for hours, or even days, often growing quite large and complex as additional workers from each colony discover the fight and join in the battle. After prolonged pulling and struggling, their vise-like grips can sever appendages; lengthy battles often result in extensive dismemberment and death. In contrast, *H. canadensis* workers run about more rapidly and inflict short, quick bites (bite-pull-release). Their speed and agility often enable them to evade attack, and their specialized mandibles quickly sever appendages and can even decapitate a foe. The success of *H. canadensis* raids against larger *L. muscorum* colonies appears to stem from this difference in fighting efficiency.

During agonistic interactions with another colony, *H. canadensis* and *L. muscorum* workers recruit nest mates by tandem running, a relatively primitive technique in which the recruiting ant leads a single follower (*1*). The two species respond to each other's recruitment, and interspecific tandem runs are common during slave raids (*9*). Although the ants were not marked in this study, it was often possible to follow the activity of individual workers and to determine exactly when the first discovery of the opposing colony's nest occurred. These observations revealed that *H. canadensis* workers, *L. muscorum* slaves, and unenslaved *L. muscorum* workers all lead tandem runs into battle, before the recruiting ant (or any other member of its colony) has discovered the opposing colony's nest. This recruitment is apparently motivated by contacts with members of the other colony, and recruits are led to the area where these encounters have occurred. Recruitment into battle (alarm-recruitment) (*10*) accounts for all of the tandem runs that occur before the occupation of the target nest by the raiding colony. Tandem runs continue to be led after the target nest has been discovered, sometimes directly to the target nest. However, the target nest is merely another scene of battle, and the behavioral context of the recruitment appears unchanged. Tandem runs have been observed during agonistic interactions in other *Leptothorax* species (*2, 11*), but an alarm-recruitment context has not been clearly demonstrated.

Alarm-recruitment probably serves as an effective means of territorial defense for *L. muscorum* colonies. In nature, the discovery of another colony's nest is probably rare, but foraging territories may frequently overlap and recruitment to such areas would be highly adaptive. It is theoretically significant that *H. canadensis* employs a similar recruitment strategy during slave raids. All other leptothoracine slave makers initiate recruitment only after the target nest has been located and then recruit only to the nest itself. Some species recruit by tandem running (*H. sublaevis* and *Chalepoxenus muellerianus*); others employ processions led by a scout and containing up to 40 followers (*H. americanus*, *L. duloticus*, and *Epimyrma goesswaldi*) (*3*). We suggest that directing raider recruitment exclusively at the target nest is an evolutionary derivative of alarm-recruitment during territorial fighting. Focusing recruitment in this way enables other slave makers to concentrate their forces in the vicinity of the target nest, a strategy which probably promotes the defeat of the target colony and enhances the proportion of brood captured. Processions are seen as an evolutionary refinement of tandem running which speeds up raider recruitment. By performing unmodified alarm-recruitment during its slave raids, *H. canadensis* empirically demonstrates the evolutionary link between the territorial behavior of nonparasitic *Leptothorax* species and the more specialized slave-raiding behaviors of other leptothoracine slave makers.

Both *H. canadensis* slave raids and *L. muscorum* territorial raids involve lengthy sieges of the target nest. Eventually, the raiders penetrate the nest, kill or drive away the adults, and take possession of the brood. After occupying the target nest, an *H. canadensis* colony may either transport the captured brood to its own nest ($N = 6$), or the entire colony may emigrate into the raided nest ($N = 4$). Either slave makers or slaves may initiate transport, and typically both are involved. Transport often occurs in both directions before one direction is ultimately chosen. Slave makers and slaves also lead tandem runs during this phase of the raid. However, these tandem runs are clearly associated with the transport of brood and adult nest mates and are led by workers which alternate transport in one direction and recruitment in the other. This transport-recruitment is probably analogous to that seen during emigrations to new nests in these and other leptothoracine ants (*12*). During *L. muscorum* territorial raids, the captured brood was always transported to the victorious colony's nest. Tandem runs occurred in a similar manner during this process.

The striking point-by-point similarities between the territorial behavior of *L. muscorum* and the slave-raiding behavior of *H. canadensis* strongly support the territorial hypothesis of the origin of slave raiding. On the basis of these similarities, the slave-raiding behavior of *H. canadensis* is the most primitive known among leptothoracine ants and demonstrates an important, previously hypothetical stage in the evolution of slave raiding.

ROBIN J. STUART
THOMAS M. ALLOWAY
Erindale College,
University of Toronto,
Mississauga, Ontario,
Canada L5L 1C6

References and Notes

1. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
2. T. M. Alloway, *Am. Nat.* **115**, 247 (1980).
3. A. Buschinger, W. Ehrhart, U. Winter, *Z. Tierpsychol.* **53**, 245 (1980).
4. A. Buschinger, *Biol. Zentralbl.* **88**, 273 (1970).
5. T. M. Alloway, *Anim. Behav.* **27**, 202 (1979); A. Buschinger and U. Winter, *Insectes Soc.* **24**, 183 (1977).
6. B. Pisarski, *Bull. Acad. Pol. Sci. Cl. 2 (Zool.)* **11**, 39 (1963).
7. A. Buschinger and T. M. Alloway, *Z. Tierpsychol.* **49**, 113 (1979).
8. Two types of arenas, with testing surfaces measuring 45.5 by 45.5 cm and 120.5 by 29.0 cm, respectively, were used. Each slave-maker colony was allowed 24 hours to acclimate to its arena before introducing a target colony. Pairs of host species colonies were placed in arenas simultaneously.
9. During slave raids, 162 tandem runs were observed. Slave makers led 49 of these, slaves led 99, and target-colony workers led 14. These include 31 interspecific tandem runs led by slave makers and 13 led by slaves. During interactions between host-species colonies, 43 tandem runs were observed.
10. E. O. Wilson, *Science* **190**, 798 (1975); *Behav. Ecol. Sociobiol.* **1**, 63 (1976).
11. J. Dobrzanski, *Acta Biol. Exp. (Warsaw)* **26**, 71 (1966).
12. R. J. Stuart and T. M. Alloway, personal observations; M. Moglich, *Insectes Soc.* **25**, 205 (1978).
13. Supported by an Ontario Graduate Scholarship to R.J.S. and a grant to T.M.A. from the Natural Sciences and Engineering Research Council of Canada.

28 August 1981; revised 18 November 1981